THE DEVELOPMENT OF THE CARPOPHORES OF CERIOMYCES ZELLERI

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(WITH PLATES 140 AND 141, CONTAINING 12 FIGURES)

A review of the literature shows that very little, if any, critical research has been done on the development of the carpophores of the fleshy pore-bearing hymenomycetes. Among the early writers, DeBary[1] mentions some of these when he divides the carpophores of hymenomycetes into two groups; viz., angiocarpic, or those forms having a marginal veil, and gymnocarpic, those forms "of purely marginal or apical progressive growth" and thus, of course, without a marginal veil. He says that *Boletus luteus* and *B. elegans* have marginal veils, while other species of this and other genera are purely gymnocarpic. Thus, with these few exceptions, he merely assigned Boletus to the gymnocarpic type of the development without a critical study of the genus. A study of the development of a species of Boletus was undertaken because it promised to throw some light upon the types of devlopment of the pileate fungi. Material for this study was collected in the fall of 1912. *Ceriomyces Zelleri* was chosen because it is so very common about Seattle, and because its gregarious habit facilitates the collection of sporophores in the young stages.

The material for the study of this species was collected in a forest of conifers on the campus of the University of Washington. It was in this place that the type specimens[2] were collected. Therefore, the identity of the species is certain.

The young fruiting bodies were found in quantities growing from a yellow mycelium which causes a matting of the conifer needles. Sections of the rhizomorphs which lead to the carpo-

[1] *DeBary, A.:* Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria. English Edition. 289–297. 1887.

[2] *Murrill, W. A.:* Pacific Coast Polyporaceae and Boletaceae. MYCOLOGIA 4: 99–100. 1912.

phores show the structure to be a pseudoparenchyma. The hyphae are 3–4 μ in diameter and the cells average 24 μ in length. The rhizomorphs are 50–90 μ in diameter. The yellow carpophores are easily recognized on the surface of this mat of rhizomorphs, and it is almost impossible for one who once knows them to mistake them for other pileate forms. The mature as well as the large immature carpophores were collected from the same mycelium. The only other species of Boletus which is common in this vicinity and might be confused with *C. Zelleri* because of its gregarious habit is *C. communis,* but the writer has never found the latter growing in this place, although the spot is often visited by him.

The material was killed in chromo-acetic acid and stained with fuchsin, using picric acid as a destaining agent. This stain gives the best results of any tried where a concolorous stain is wanted to show differentiation in protoplasmic content. A large number of small carpophores of different sizes were collected. The size of the carpophores does not necessarily correspond with the degree of development, so it is not possible to forecast the stages of growth by the size of the plants. The smallest undifferentiated fruit bodies sectioned were about 1 mm. in diameter, while some of the larger ones were 1.5×3 mm. however, others in which differentiation had begun to show plainly, measured 1×2 mm.

The first stages show no differentiation (Fig. 1). There is no indication of a universal veil, either by differential staining or by the usual coating of loosely woven hyphae. In fact, as the later stages show, there is *no* veil, either universal or partial; the carpophores are thus entirely gymnocarpic and DeBary was correct in his inference that some of the Boleti are gymnocarpic. The young undifferentiated carpophore elongates vertically and becomes three or four times longer than broad. There is no differentiation of tissue during this elongation. The carpophore is still a homogeneous mass of hyphae, their general direction being vertical in the inner part and parallel with the surface in the peripheral portion. The first differentiation begins as a superficial, darkly-staining, annular region extending around the carpophore a short distance from its summit (Fig. 2). This area grows centripetally from the periphery and slightly upward, forming what is geometri-

cally the surface of a truncated cone. This feature is the demarcation of the pileus fundament above and the stipe fundament below. However, before this differentiation is complete, the hyphae above in the pileus fundament begin a radiate growth in the peripheral portion and the palisaded cortex of the pileus is formed. Figure 3 shows this palisade of an older pileus. The ends of the excurrent hyphae are somewhat tufted, and no doubt this feature brings about the characteristic velvety surface of the pileus. This palisade extends over the summit of the carpophore and down over all sides of the pileus fundament to the deeply staining area. The hyphae in this deeply staining portion extend vertically through it. This area resembling a truncated cone becomes a plane of cleavage, and the hyphae break apart here forming a superficial annular furrow. The cleavage takes place throughout the area simultaneously; *i. e.*, it is neither decidedly centripetal nor centrifugal. Figures 4 and 5 show different stages in the cleavage process, and figure 6 is the cleavage plane of figure 5 highly magnified. After the annular furrow is formed, the ends of the hyphae which were cut off above project downward, forming a palisade which is the primordium of the hymenium. The tips of these hyphae become blunt and form a smooth surface which is always free to the exterior after its formation. It is clear, therefore, that the hymenium is exogenous in its origin.

The superficial hyphae of the stipe keep the same general relation to the periphery which they sustained in the undifferentiated carpophore. However, the ends of the hyphae which were cut off below the annular furrow project upward, forming a palisade on the lower surface of the furrow. As the stipe elongates and the furrow broadens, this palisade is carried down to form the cortex of the upper part of the stipe. Thus, the cortex of the lower part of the stipe is composed of hyphae which extend parallel with the surface, while the portion of the cortex of the stipe near the pileus is of palisaded hyphae. Figure 7 shows this feature in the cortex of the stipe. The pileus increases in size by a centrifugal growth at the margin, the hyphae turning upward and downward at this point adding to the palisaded surface and the primordium of the hymenium, respectively. At this stage the hymenium is plane and quite horizontal.

A little later, slight anastomosing elevations of the hymenial primordium appear. These are formed by a differential downward growth of the hyphae in these regions (Fig. 8). As the hyphae forming these elevations grow downward, they turn out horizontally on both sides to form the hymenium in the pores. The hymenium stains deeply while the central part or trama takes comparatively little stain. The trama is a pseudoparenchymous tissue. After it has grown down for some distance, the trama begins to broaden by a diametrical growth of the hyphae, which also become loosely associated. For this last reason, the pores of the mature carpophores can be easily torn apart or separated from the trama of the pileus. The subhymenium appears later, made up of an interwoven mass of hyphae tightly crowded together. The number of basidia is increased by the branching of the hyphae at the clamp connections in the subhymenium. The hymenium lines the pores only. The mouths of the pores are sterile. Figures 9 and 10 show vertical and transverse sections of the pores, respectively.

To sum up the development of the carpophore of *Ceriomyces Zelleri* Murrill, there is a homogenous mass of tissue which is differentiated simultaneously into pileus and stipe by a cleavage plane which gives rise to an annular furrow. The hymenium is formed in the roof of this furrow and is exogenous in its origin. *Ceriomyces Zelleri* is gymnocarpic because there is no marginal veil.

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EXPLANATION OF PLATES CXL AND CXLI

Photomicrographs by Homer O. Blair

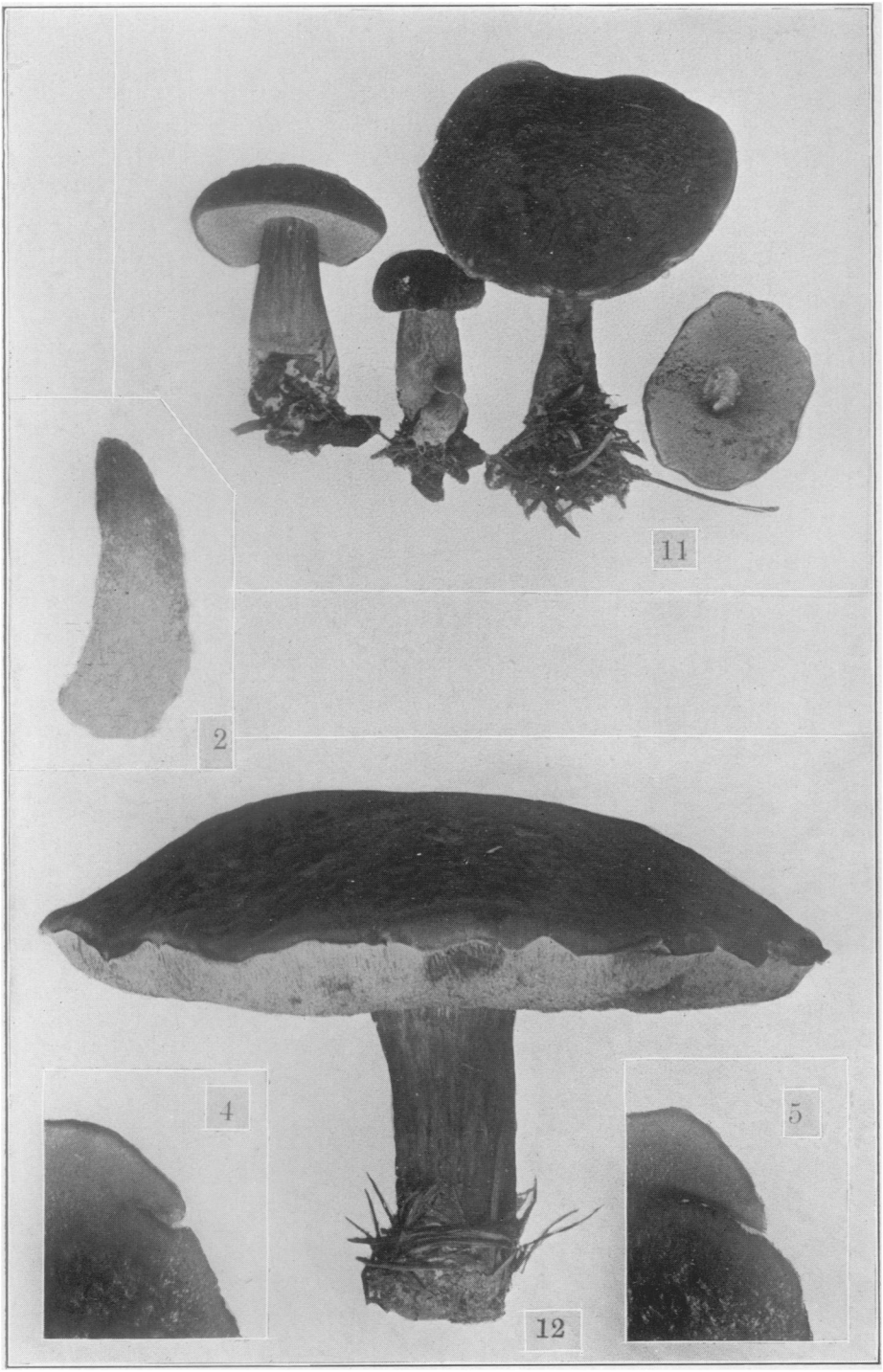
Figure 1. A small undifferentiated carpophore of *Ceriomyces Zelleri*. × 30.

Figure 2. The first differentiation in the carpophore, showing deeply staining ring in the periphery. × 20.

Figure 3. A portion of the palisaded cortex of an older pileus with the excurrent hyphæ tufted. × 250.

Figures 4, 5. The cleavage plane in different stages of cleavage. × 12.5.

Figure 6. A portion of the cleavage plane shown in figure 5 much enlarged. × 250.



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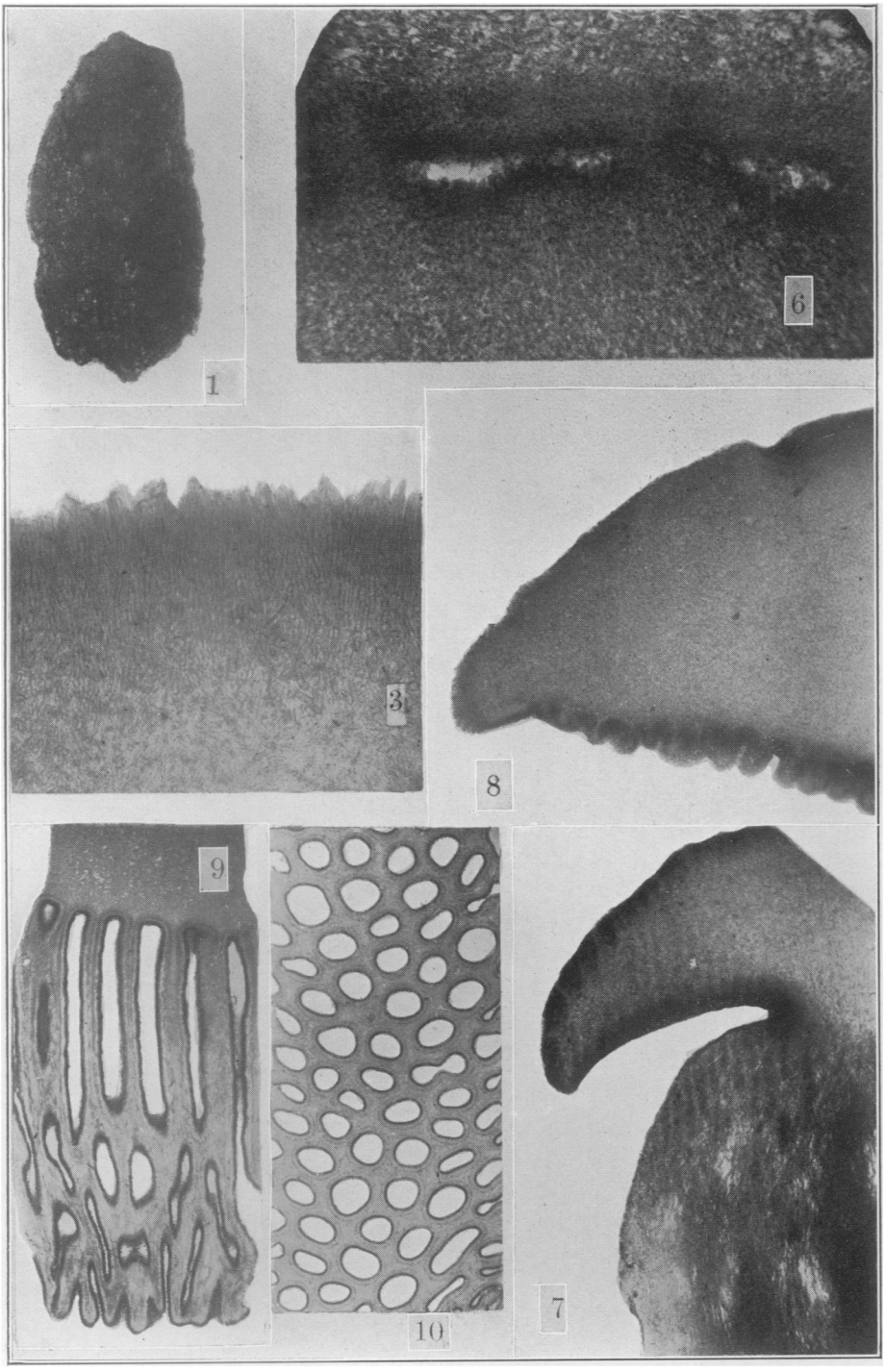

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Figure 7. A portion of a vertical section through the stipe. The junction of the palisaded cortex of the upper portion of the stipe and the portion of the cortex where the hyphæ are parallel with the surface is shown. × 25.

Figure 8. The first folding of the hymenial primordium. × 40.

Figure 9. A longitudinal section of the pores showing the trama, subhymenium, and hymenium. × 30.

Figure 10. A cross section of the pores. × 30.

Figure 11. A group of nearly mature carpophores. × 1.

Figure 12. A mature carpophore of *Ceriomyces Zelleri*. × 1.